# The Journal of HEREDITY

NO SMOKE WHERE THERE'S WILDFIRE
(SEE PAGE 35)

The South American Rubber Tree

Fowl Diet and Feather Length

Webbed, Joined, and Extra Toes

Puerto Rico's Progress

VOLUME 38 FEBRUARY, 1947 NUMBER 2

# The American Genetic Association

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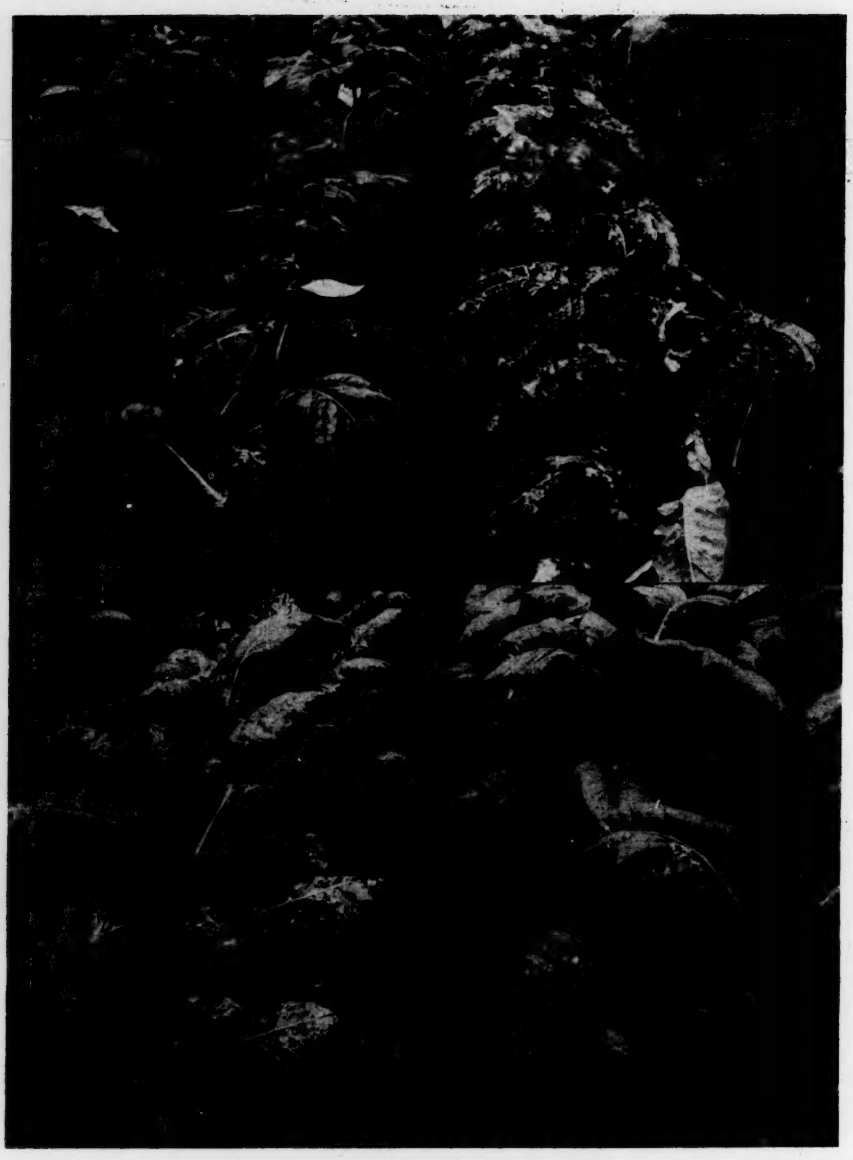

**RESISTANCE COMPLETELY DOMINANT**

**Figure 1**

Above are shown adjoining rows of the *longiflora-tabacum* hybrid TL106 and the commercial tobacco variety Pennsylvania Broadleaf. Below are adjoining rows in the same field, of Havana 211 and the $F_1$ hybrid between Havana 211 and TL106. All plants were repeatedly sprayed with cultures of the wildfire bacterium, *P. tabaci.* Note that the Havana 211 $\times$ TL106 is just as resistant to wildfire as TL106 itself. Dominance of resistance to wildfire is virtually complete. Since no commercial tobacco varieties are resistant to this devastating disease, the transfer of resistance from *N. longiflora* has obvious utility in tobacco breeding programs.

# A WILDFIRE RESISTANT TOBACCO

E. E. CLAYTON*

EARLY records of tobacco culture in the United States refer to red rust, brown rust, and black rust as very destructive diseases. It is probable that these "rusts" are the bacterial diseases now known as wildfire and blackfire, and that they have been present in this country for a long time. Both were extremely prevalent between the years 1917-1925 and caused heavy losses in all the major tobacco producing areas of the United States. At that time the causal organisms were identified as two species of bacteria, *Pseudomonas tabaci* (Wolf and Foster) Stapp and *P. angulata* (Fromme and Murray) Stapp. During the period 1926-1945 these diseases were less destructive and disappeared completely from some areas. In other areas, such as Pennsylvania, wildfire has continued prevalent with repeated severe outbreaks. Recently wildfire has reappeared in areas where for a period of years it had not been observed and the same has been true of blackfire. There are many indications that these diseases are on the increase, and that another period of widespread outbreaks over large areas may be an immediate prospect. This makes the problem of control of critical importance. Abroad wildfire has been particularly destructive in parts of Europe and South America.

As the result of much careful work, measures for the control of bacterial leaf spots have been developed that are fairly effective in the plant beds. No way has been found to control the diseases after the plants are growing in the field. Unfortunately it is in the field that wildfire and blackfire do the most damage, and seed bed control is much less important. Many workers have made observations on varietal resistance and no high degree of resistance has been found.[1,6] The writer, begining in 1934, made a study of collections of *Nicotiana tabacum* L. from various parts of the world and not a single highly resistant genotype was discovered. Many were resistant if the disease attack was slight to moderate, but this resistance broke down under severe disease conditions. Unfortunately the cultural practices that must be followed to produce certain desired commercial types of tobacco—high fertilization and low topping—are just the ones that most favor leafspot attack. Observations on the two diseases in the field indicated that there was a close association between wildfire and blackfire resistance. So close was this correlation that from the viewpoint of disease resistance it appeared that wildfire and blackfire might be regarded as the same disease. In this connection recent studies have shown that *P. tabaci* and *P. angulata* cannot be separated on the basis of morphology or by cultural, physiological or serological tests.[2,7] The lesions caused by the two on young plants, however, are very different, so they can be readily separated in this way. The wildfire parasite is the more aggressive and it has been used as the test organism in this work.

### The Cross of *Nicotiana tabacum* with *N. longiflora*

*Nicotiana tabacum* is one of the two species cultivated in a rather large genus. Some of the wild species of *Nicotiana* are immune to wildfire.[1] This was true of all the plants in a collection of *N. longiflora* received from Dr. T. H. Goodspeed of the University of California. Unfortunately none of the wildfire-resistant species crosses readily with *N. tabacum*. Attempts by a number of investigators to cross *N. tabacum* with *N. longiflora* have been unsuccessful. In 1938 a large-scale effort was initiated

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**RESISTANT PARENT AND HYBRIDS**

**Figure 2**

Above is a plant of *Nicotiana longiflora,* a form having only one characteristic of agronomic importance—immunity to infection by the wildfire bacterium. Hybrids between *N. longiflora* and *N. tabacum* are hard to make and the few obtained have been sterile and of low viability. One of these produced shoots from a callus which were vigorous, and highly fertile when backcrossed to tobacco. Two of the backcross plants are shown below, showing segregation for *longiflora* and *tabacum* characteristics. Some of the *tabacum* segregates were highly resistant to wildfire.

using 4*n* plants as parents in the hope that fertile tetraploids would be produced. Practically all the seedlings secured were defective and died early, just as had been the case when crosses had been previously attempted between diploids. A number of the hybrid plants made a weak growth and ultimately flowered, but all were completely sterile. Then came an unusual development. After 18 months three of these plants produced galls of callus tissue about 1½ inches in diameter at the ground surface. The tops died back to the ground. To our astonishment, new shoots grew from the gall tissue. These shoots were vigorous. One plant with an original top less than two feet tall, produced a shoot that grew to a height of 19 feet. This plant was self-fertile but unfortunately the progeny showed no wildfire resistance. The second plant remained completely sterile. The third plant was self-sterile but set seed freely with *N. tabacum* pollen and from these backcrosses a large progeny was grown.

*Nicotiana longiflora* was wildfire immune (Disease index 0) and *N. tabacum* susceptible (Disease index 4).* Out of 490 plants of the backcross grown to maturity and inoculated a great diversity was observed in morphological characters and in wildfire resistance. Only 19 plants were rated highly resistant (Disease index 1). No detailed cytological work could be undertaken, but pollen smears and microspore MI counts of this material showed 25 to 28 chromosomes, with every indication of regular pairing. These hybrids gave us our first success in breeding *Tabacum* type plants resistant to wildfire.

### Testing for Wildfire Resistance

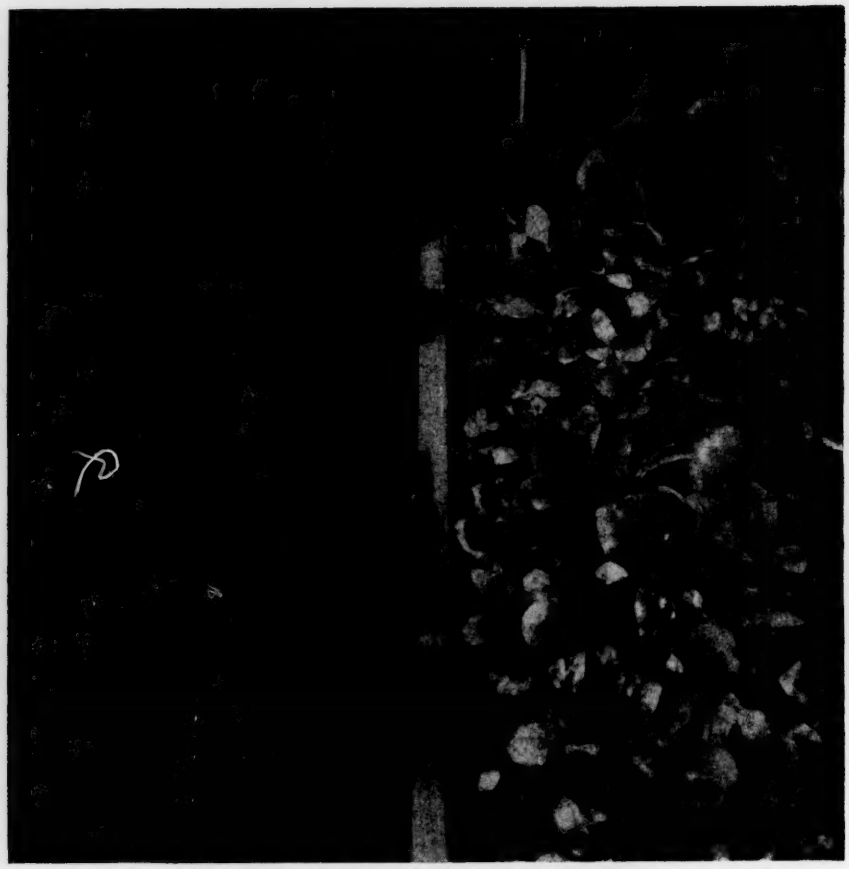
The $F_2$ seed of selected lines was planted in the field in 1942. A number of plants in one line remained completely free of wildfire infection throughout the summer. One of these plants was given the number TL 106. The inoculation and selection work was continued with this and similar lines through the $F_3$, $F_4$, and $F_5$ generations. Each year the experimental plots were inoculated with the wildfire organism. There was a steady decrease in the amount and the severity of the wildfire infection. In 1944 the $F_5$ lines of TL 106 showed only a trace of infection on a few plants. The $F_6$ selections were tested in 1945, and again in 1946, and they remained completely free of wildfire. The importance of subjecting this material to the most prolonged and severe tests has been recognized. Each year inoculations were started in the plant bed as soon as the seedlings were above ground. At this stage plants are easily killed by wildfire, and stands in check plots were often reduced more than 50 percent.

There was no measurable stand reduction in TL 106 plots. Repeated inoculations while the plants were in the seed beds produced no leaf lesions. In the field tests, inoculations were continued over a period of weeks both before and after topping and again none of the plants became infected. Plants were fertilized heavily and other conditions were provided to favor disease development. It appears consequently that TL 106 is highly resistant to wildfire from the earliest seedling stage on through its growth to time of harvesting. The resistance is comparable to that possessed by *Nicotiana longiflora*.

A high degree of disease resistance that is maintained in all stages of plant growth is a very exceptional phenomenon. Thus *Nicotiana* species reported immune to blue mold[4] are quite susceptible in the early seedling stages. Existing black shank, wilt, and black root rot resistant varieties are all susceptible to attack as seedlings and do not develop their full resistance until some weeks after they have been transplanted into the field.

TL 106 was one of a number of selections made in 1942 for wildfire resistance from the same material. Inoculation and selection work was continued

*Degrees of susceptibility to wildfire were recorded as follows: Immune 0; Highly resistant 1; moderately resistant 2; slightly resistant 3; susceptible 4.



**WILDFIRE RESISTANCE IN THE SEEDBED**

**Figure 3**

The left half of the flat is planted with seeds of the hybrid TL106 × Madole; the right half of the flat is sown with seed of the Madole variety. The entire flat has been inoculated repeatedly with cultures of the wildfire bacterium (*P. tabaci*). From germination to the maturity of the plant, the TL106 selection and hybrids of it with susceptible tobacco varieties are highly resistant to wildfire infection.

in subsequent years but in 1946 all lines except TL 106 were still segregating for wildfire resistance. Hence at the present TL 106 is the only homozygous wildfire resistant line that has been secured.

### Reaction of TL 106 to Watersoaking

Watersoaking of leaf tissues, produced by rain and high humidity, has been shown to be an important factor in the epidemiology of wildfire.[3,5] Hence the reaction of TL 106 to watersoaking is of especial interest. In 1945 and again in 1946 there was one period of extensive watersoaking development, following heavy rains, while the plants were in the beds. Prior to this time, all plants of the wildfire susceptible checks had developed numerous small lesions. The watersoaked areas appeared around these

**HETEROSIS OF WILDFIRE RESISTANT HYBRIDS**

**Figure 4**

To the left is a row of Havana 211, a standard tobacco variety. To the right is a comparable row of $F_1$ hybrid Havana 211 × TL106. The $F_1$ plants at the right weighed 51 per cent more and were 27 per cent taller than the Havana 211 plants. The number of leaves was the same.

lesions and were rapidly invaded by the bacteria. Large dead areas resulted. The TL 106 plants had no lesions and showed no watersoaking.

### Wildfire Resistance of the $F_1$ Generation

TL 106 was crossed with five standard varieties of tobacco and the $F_1$ populations were tested in 1946. All $F_1$ plants showed marked heterosis in the plant bed. Disease counts were made after repeated inoculations. Of 1350 $F_1$ plants only five showed infection. A count of 1,000 check plants showed 100 percent infection, and 600 TL 106 plants similarly exposed were healthy. Large field plantings were made with $F_1$ plants and these remained practically free of infection throughout the season. Close examination showed a few faint lesions, but if there was any difference in the resistance of the $F_1$ and the TL 106 parent it was extremely slight. This type of wildfire resistance therefore behaves as a complete dominant. The $F_1$ plants in the field continued to show marked hybrid vigor. All plants of the susceptible

parent variety were larger than comparable TL 106 plants, and each $F_1$ was consistently larger than the susceptible parent.

Green weights of the $F_1$ plants were compared with those from the susceptible parent. Five lots of $F_1$ plants weighed 25, 28, 33, 34, and 51 percent more than the paired controls. Heterosis is not uncommon in tobacco, but it is rarely as pronounced as with the wildfire-resistant hybrids.

Some studies have been made with $F_2$ populations. Many of these plants are wildfire resistant and some closely resembled susceptible parents in appearance. No information has yet been secured on cured leaf quality.

### Resistance of TL 106 to Blackfire

During each of the past three years plantings of TL 106 were inoculated with *P. angulata,* the organism causing blackfire. No infection was secured on the TL plants while check plantings of commercial tobacco were heavily infected. Tests with blackfire have been on a comparatively small scale, with 400 to 600 plants in the field each year. The results indicate that TL 106 is highly resistant to blackfire as well as wildfire.

### Description of TL 106

TL 106 is uniform and has the growth appearance of *Nicotiana tabacum.* In 1946 the average measurements were, plant height 44.2 inches, leaf number 19.1 and leaf size 11.45 by 19.9 inches. These measurements were slightly less than those of commercial tobacco varieties grown under the same conditions. TL 106 suckers somewhat more freely than ordinary tobacco but in other respects it has no growth characters that would be counted definitely undesirable.

It is as susceptible as ordinary tobacco to such diseases as, black root rot (*Thielaviopsis basicola*), blue mold (*Peronospora tabacina*), brown spot (*Alternaria longipes*), frogeye (*Cercospora nicotianae*) and mosaic. It is highly resistant to wildfire (*Pseudomonas tabaci*) and blackfire (*Pseudomonas angulata*) and is of value as a breeding stock. Seed is available for distribution to research workers.

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## Yellow Mice and Differential Mortality

A correspondent raises the question whether the decrease in weight of ageing yellow mice as reported by Dickie and Woolley (Journal of Heredity, December 1946) might not be the result of a differential mortality among the yellow mice whereby the more obese mice tend to die earlier than those accumulating less fat. Inasmuch as the graphs (Figures 6 and 7) presented only averages, he wonders whether the data on individual yellow weights shed any light on this point.

Acording to Dr. Woolley, individual yellow mice *do* decrease in weight with age. At this time, there is no evidence of a significant relationship between maximum weight and longevity. Weight records are still being kept on individual yellow mice and perhaps when more data have accrued, it may be possible to illuminate this point more fully.

# DIET-INDUCED FEATHER MODIFICATION IN THE FOWL

## Sickle and Feather Growth in Thiouracil-treated and in Japanese Long-tailed Chickens

MARY JUHN AND M. A. JULL
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FOR hundreds of years much interest has been manifested among poultrymen and biologists in the extraordinary length of the sickle and saddle feathers attained by the so-called "Japanese Long-tailed" fowl, otherwise variously known as Tosa, Phoenix, and Yokohama. The origin of this variety is shrouded in mystery. The most reliable reports indicate that its was known in Korea before A.D. 1000 and that the finest specimens were developed in Shinowara, a small village in the Province of Tosa, on the island of Shikoku.

Although the "Japanese Long-tailed" fowl has been bred in Japan for centuries, the term "Long-tailed" is a misnomer because the long-tailed effect is the result of the unusual length of the sickle and saddle feathers whereas the main tail feathers approximate the length found in such breeds as the Black Sumatra.

Much speculation has been indulged in by numerous writers of poultry lore concerning the origin of this interesting characteristic exhibited by a modern breed of domestic fowl. The literature has been searched carefully for an authentic explanation of the development of the length attained in this breed which differentiates it from all other breeds of fowl.

### A Review of the Literature

Chamberlain[2] cites an instance of sickle feathers 18 feet long although about one-half of that is the usual length. Romanes[9] and Weismann[13] held that the character is the result of selection.

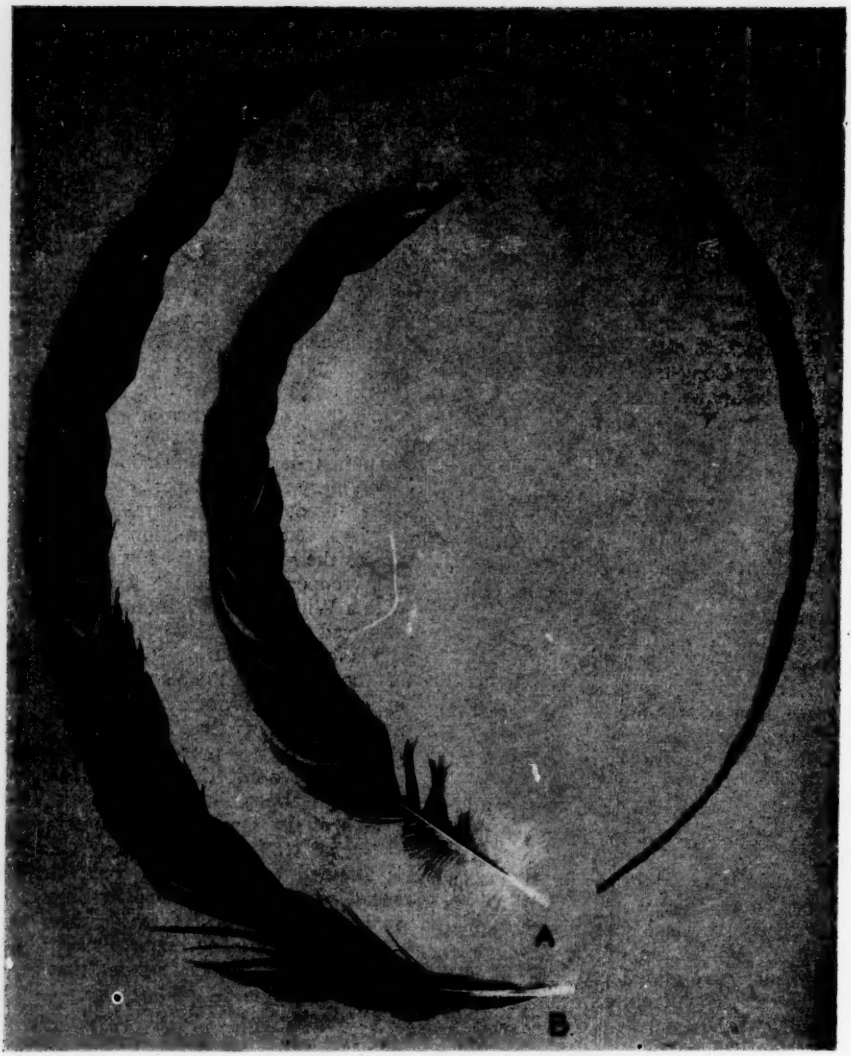
Cunningham,[4] acting upon the suggestion that pulling the feathers gently every morning stimulated their growth, used two cocks for test purposes. The sickle feathers of one cock were pulled gently at regular intervals and the sickle feathers of the other cock were not pulled. He observed that the pulled feathers did not grow at a more rapid rate but continued growth for a longer time. When feathers stopped growing, he pulled them out and concluded that "The more important part of the stimulation is not the mere pulling of the feathers, but the extraction of it which causes the growth of its successor."

Davenport[5] crossed a Yokohama male with a White Cochin Bantam female and observed that the male progeny had sickle feathers about one-third the length of those in the Yokohama sire. The male progeny, however, had not reached maturity when the observation was made, so that it is possible that the sickle feathers in adult progeny would have attained approximately one-half the length of the same feathers in the sire.

Beebe[1] states that the greatest length is attained by the central sickle-shaped rectrices and as these feathers increase in length, the roots of the feathers become thicker and stronger. According to Beebe, "It has been proved that constant gentle pulling and stroking of the feathers has a certain effect in making the feathers grow somewhat more rapidly, but this is only an unimportant indirect stimulation, not used by the Japanese. As a matter of fact, there is no secret connected with these birds, and their great length of feathers is as normal a product as the crests of other breeds."

Robinson,[8] although giving some cred-

*Scientific paper No. A150, Contribution No. 2043, of the Maryland Agricultural Experiment Station (Department of Poultry Husbandry).




**STIMULATION OF SICKLE FEATHER GROWTH**

**Figure 5**

Two sickle feathers from an $F_1$ male of the cross New Hampshire male $\times$ Brown Leghorn female. *A* is a mature sickle feather produced before treatment. *B* is a comparable feather produced during the time the fowl was fed thiouracil. The thiouracil has the effect of increasing the size of the thyroid gland and lowering metabolism. It is suggested that the Japanese Yokohama fowl is stimulated to produce prodigiously long sickle feathers by a diet of cabbage, which experiments with rabbits have proven to be highly goitrogenic. The photographs for this paper were prepared by Mr. John Spurbeck to whom the authors wish to express their appreciation and indebtedness.

ence to the theory that the great length of the feathers was attained by a systematic slight pulling on the feathers, suggested that this method was fruitless except in birds having an inherited tendency to prolonged growth of the feathers concerned.

Against the feather-pulling theory as an explanation of the great length of feathers attained in Yokohamas, is the statement by Beebe[1] that after the second year "there appears to be no moult of the tail-coverts and central rectrices, and within four to six years these feathers have attained an enormous length." That the diet of the birds may have something to do with the growth of the feathers involved is indicated in Beebe's statement that the Yokohamas are fed with great care and that unhusked rice, cabbage, and other vegetables are included in the diet. Shakespeare[11] is authority for the statement that "The secret is supposed to be in the foods fed during the time the birds are changing, or putting on their adult plumage."

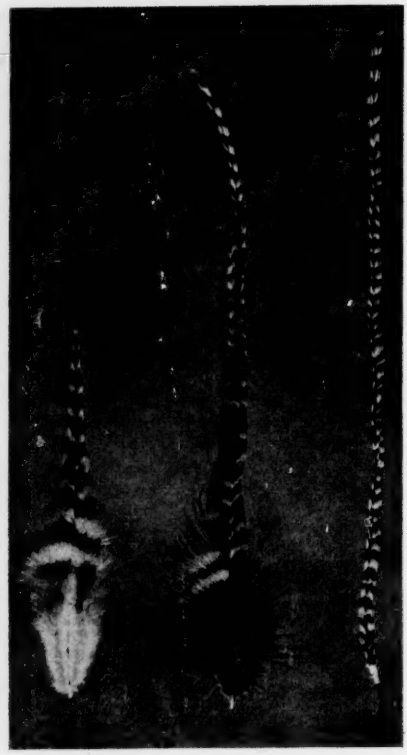
### The Effect of Thiouracil

Ascribing to some dietary component a participating action in the development of the feather length extremes in the Yokohama becomes suggestive in view of certain recent findings in male fowl placed upon a thiouracil diet. Adult cocks fed the drug at one-half per cent levels of the dry feed, in time develop certain similarities with the ornamental bird. Photographs of the Yokohama (See Jull,[7] pp. 418-19) show a relatively small comb but long and pendulous wattles and earlobes. The neck hackles are long and delicately narrow as also are the saddle hackles and the sickles where the greatest increases in length are achieved. These features of the head-furnishings of the Yokohama are repeated, to some extent, in the thiouracil-treated cock who also shows a narrowing of the feathering together with lengths which, while not approaching those in the ornamental bird, are nevertheless considerable. Furthermore, some feathers of the thiouracil-fed fowl were found to show a peculiar twist, causing opposite feather-vane surfaces to tend to succeed each other along the axis,[6] and this property could also be recognized, although not in the same degree of severity, in a sickle feather of the Yokohama that we were able to examine through the courtesy of Dr. Alexander Wetmore of The Smithsonian Institution of Washington.

The development in length that may be achieved in the feathering of thiouracil-treated adult cocks is illustrated in the photographs accompanying this paper. Figure 5 contrasts a normal sickle (*A*) with a thiouracil-modified sickle (*B*) of $F_1$ male 689, from a New Hampshire male × Brown Leghorn female mating. The bird was hatched July 18, 1944, and placed on a 0.5 percent thiouracil* diet from January 23, 1945, to October 12, 1945, and again from December 19, 1945, on. In the intervals the bird was fed the regular station mash. By December 19, 1945, the two main sickle feathers each measured 25.5 inches and were still in growth, as shown in an examination of the bases. By May 23, 1946, the right sickle was found to have been lost; the left sickle, having terminated growth, was removed. At that time the feather measured 33.5 inches. The apical portion was narrow and reddish in color; toward the base, however, the feather width increased with a simultaneous return of the normal metallic green, indicating the onset of refractoriness toward the drug which was fed at a constant level. Toward the extreme base the thiouracil-effect became manifest again both in pigmentation and structure.

In Figure 6 are shown control and test saddle feathers of $F_1$ male 709, from a Brown Leghorn male × Barred Plymouth Rock female mating. This bird was hatched July 18, 1944, and was fed thiouracil from January 23, 1945, to January 5, 1946, the date of its death.

*The thiouracil used was obtained through the kindness of Dr. Mark Welsh, Lederle Laboratories, Inc.



**COMPARATIVE SADDLE FEATHER LENGTHS**

**Figure 6**

These three feathers are from a male offspring of a Brown Leghorn × Barred Plymouth Rock mating. *C* shows a feather of normal length before the bird was placed on thiouracil. *D* was plucked at its full modified length. As is evident from the immature feather base, *E* would have grown still longer if the bird had not died.

Figure 6*C* illustrates the normal condition; *D* and *E* are two examples of the modified feathers that were collected at autopsy, showing the characteristic thiouracil effect. In *D*, the length was greatly increased and there was a simultaneous narrowing of the vane and decrease in barbulation; growth was terminated. The feather shown in *E*, also very long and somewhat more narrow, had not yet completed growth, as is evident in the condition of the feather base.

## Discussion

Growth is prolonged in the feathers of the thiouracil-fed bird and the successive periods of growth tend to become further extended in later feather generations of long-time treated birds.

The modifications resulting in the regenerating feathering of thiouracil-treated fowls are apparently mediated through the effect the drug exerts upon the thyroid; *i.e.*, by increasing the size of the gland but depressing the basal metabolism. (For a recent discussion of these relations and full references, see Schultze and Turner,[10] especially pp. 22-29.) Various dietary factors have earlier been found to prove goitrogenic; among such observations, those of Chesney, Clawson and Webster,[3] and Webster and Chesney,[12] that cabbage is a powerful goitrogenic agent in the rabbit, are most interesting because of the reported inclusion of this vegetable in the diet of the Yokohama at the time birds are selected for feather length growth. They then receive special care and are closely caged.[1]

The low fertility of the Yokohama as well as the appearance of its feathering suggest a bird with a relatively inactive thyroid, and in view of the similarities that have been noted between the thiouracil-treated and the ornamental bird, it does not perhaps appear too far fetched to suggest that a diet rich in cabbage may, in the bird, prove to have some goitrogenic action and participate in the development of the extreme feather lengths. Other factors undoubtedly are important, such as in the first place genetic composition, since feather length is a trait that is known to vary greatly in different breeds. The age of the ornamental bird at the time it is narrowly confined, at about two to three years of age[1] also probably plays a part since feather length as such tends to increase with age. Finally, the special care and close confinement must be highly important since in ordinarily caged birds the tail feathers tend to break off. The growth of the sickles to the lengths recorded in the thiouracil-

fed male 689 (Figure 5*B*) were made possible in part through the softer-than-normal texture of the experimental feathering.

**Summary**

A comparison is drawn between the appearance and the lengths of the feathering in Japanese Long-tailed cocks and in hybrid cocks fed upon 0.5 percent thiouracil. It is suggested that some component of the diet of the ornamental bird, possibly cabbage, may have an effect similar to the drug and be a participating factor in the achievement of its feather lengths.

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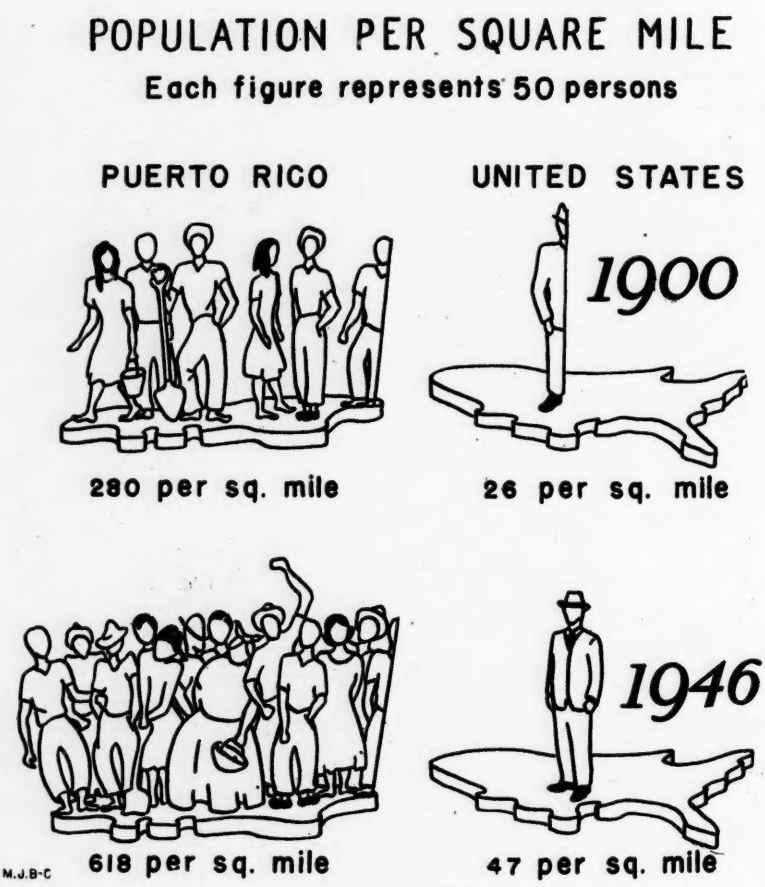
# PUERTO RICO MARCHES ON

THE Island of Puerto Rico has increased in size not one whit since American occupation in 1898; but during that time the population has more than doubled. Mention has been made more than once in this Journal of some of the difficulties which have stemmed from this situation. *The Population Bulletin* for May 1946 brings us up to date in the continued story of privation and despair that this sorry story of evasion means to the people involved.

As mouths have increased in number, wherewithal to fill them has not kept pace. The average Puerto Rican gets less than a third of the by no means adequate average protein diet of a citizen of the continental United States. Other nutritional deficiencies are proportionately bad. Four out of every five workers on the Island average less than $10 per week income.

This parlous situation cannot be attributed to an absence of interest in the problem. It is quite generally recognized as being alarming; there is even no lack of constructive suggestions. Surveys of the dilemma and suggestions for action have recently been made by three different agencies: The Puerto Rico Planning, Urbanizing and Zoning Board, the U. S. Tariff Commission, and the Puerto Rican Legislature. There is unanimous agreement that the central problem is the density of population and its increasingly rapid rate of growth which in recent years has been exceeded hardly anywhere in the world. The population of two million will reach four million by 1980 if recent increases continue. In a predominantly mountainous country, the average density of over 600 per square mile makes Puerto Rico—in terms of inhabitants *per arable square mile*—one of the most heavily peopled regions on earth. There are now over two persons for every arable acre (Figure 7).

The U. S. Tariff Commission points




**STANDING ROOM ONLY**

**Figure 7**

Since the turn of the century the already crowded people of Puerto Rico have more than doubled their numbers. There are now about two persons per arable acre of Puerto Rican land. Soil scientists consider that more than two acres of arable land per person are essential for adequate minimum dietary needs.

out that even were half the Island's population to emigrate to less congested regions, this would be only a temporary relief in the face of existing birth and death rates. "Efforts to bring about such a decline [in the birth rate] recommends itself as the most worthwhile course for the Island to pursue. For it—both in its own economic interests and in those of the United States as a whole." (U. S. Tariff Commission, Reports on the Economy of Puerto Rico, March 1946.)

The Planning Board Report furnished much data to support this idea and made some very practical suggestions:

> That people and their resources may be in equilibrium is the goal of every society. This equilibrium, however, need not be static. It can advance as science and technology, education and social responsibility—and in some

societies, war—increase the opportunities for adjustment at a high level. Through such programs as health, education, and better housing the human resources of Puerto Rico can and should be developed so that they can contribute to the expansion of production. But it has been indicated as doubtful that production will be able to overtake population. If this is true and if it is considered really desirable to attain the minimum standards of living, then it would appear that population itself might be directly affected. It is no more rational to consider population trends fixed than production trends; both are subject to reason. . . . Although its [The Maternal and Infant Hygiene Bureau's] work has been partially restricted by law and its funds and personnel limited the case load of reporting mothers has risen to 36,000 in 1942. Each case is fully documented and carefully followed up, and the education of the mother is considered of equal importance with, if not of more importance than the actual supplying of contraceptive material.

No cost estimates are available, but if it is assumed that one quarter of the entire expenses of the Bureau can be directly or indirectly attributable to this program, the annual cost would be approximately $7.50 a case. It is not supposed that anything like full coverage of all 'health' cases would in practice be desirable, even if feasible, but a continued expansion of the present work by 10,000 to 20,000 cases a year should be possible, at an annual increased cost of $75,000 to $150,000, attaining an eventual annual total of only $1,550,000 for 200,000 cases. This would indeed be a very small sum to pay annually for the stabilization of Puerto Rico's population long enough to allow other more basic factors such as increased living standards and universal education to affect the birth rate. (*A Development Plan for Puerto Rico,* Puerto Rico Planning, Urbanizing and Zoning Board, January 1944.)

Rarely has a public agency issued a more surpassing understatement and one which more "deserves the earnest consideration of all American citizens living in Puerto Rico or in the continental United States." If the growth of the Island's population cannot be brought under control by this means or others, the dollars and cents cost in the end will be vastly greater than this and the suffering and privation will defy computation.

Even more recently the President of the Puerto Rican Senate, Luis Munoz Marin, said in part:

". . . In no place in the world can 630 persons per square mile subsist, except at very low levels, on an agrarian economy. The present Legislature of Puerto Rico . . . is trying to deal with the economic problem of Puerto Rico along the following lines: increased agricultural production and industrialization . . . to keep up with the growing population . . . and to improve the standard of living of the common man to the point where, through educational and other factors, the birth rate begins to decrease. (In this connection it should be pointed out that the size of Puerto Rican families is smaller above the $800 a year level of income than below that level. But 70% of Puerto Rican families are far below that level still). . . . It is along this line that we expect to accomplish the hard task of developing our production to the point where three million Puerto Ricans —the probable figure—can by 1960 support themselves without other aid than their own effort, without a lag of chronic unemployment and at a level, modest but sufficiently decent, to bring about a decrease in the birth rate. . . ."

In contrast to the more dynamic approach of the Planning Board, the Legislature seems committed to a first-things-last approach that is wholly Utopian. But that need not be fatal; the important fact is that there is increasing realization that population is the key to the Island's troubles. Once this idea begins to sink in, reason and a decent regard for the sufferings of those who have to try to subsist on less than an acre of not-too-arable land, will begin to evolve workable solutions.

In the continental United States we seem still to prefer blindman's buff. A syndicated news article on Puerto Rican population problems appeared in the Sunday newspapers in January. Claiming that no accurate figures were available, this story made the astounding assertion that in 1946 400,000 Puerto Ricans had come to the mainland—most of them to New York City. Actually, the Puerto Rican Department of Health publishes statistics regarding the number of persons leaving and entering

Puerto Rico. This shows that in 1946, 288,726 persons left Puerto Rico; 222,940 arrived on the Island, a net loss of population for the year of 65,786. During the year, 89,024 births were recorded, and 27,440 deaths, a net gain of 61,584 through natural increase. Hence immigration did serve to keep the population approximately stationary for the year. Inadequate as this solution is on a permanent basis, it helped for the time being. Incidentally the provisional birthrate of 42.8 and deathrate of 13.3 gives a net increase of 2.9 per cent per year, one of the highest natural increase rates on record. This would lead to a doubling of the population in about 25 years, even sooner than contemplated by earlier estimates.

Surely a man from Mars, confronted by the strange paradoxes found in Puerto Rico, could do no less than raise his eyebrows—even shake his head sadly—when told that such sensible suggestions as those of the Planning Board have fallen on ears as deaf as those which have ignored all the earlier repetitions of this same idea. That an "age of science" which is trying to deal with the world-wide problem of the atom bomb, seems powerless to take any rational and humane steps on a scale in the least likely to solve this lesser problem, might seem incredible to an interplanetary visitor. But there is the record—nearby 700 people per square mile, and square meals out of the question for most of them. "What," our Martian visitor might ask, "is the use of all your skills, and knowledge and gadgets, if you can't use knowledge readily available to do something *effective* to help these people?"

R. C.

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## Books and World Recovery

The desperate and continued need for American publications to serve as tools of physical and intellectual reconstruction abroad has been made vividly apparent by appeals from scholars in many lands. The American Book Center for War Devastated Libraries has been urged to continue meeting this need at least through 1947. The Book Center is therefore making a renewed appeal for American books and periodicals—for *technical and scholarly books and periodicals in all fields* and particularly for *publications of the past ten years*, including complete or incomplete files of the JOURNAL OF HEREDITY.

The generous support which has been given to the Book Center has made it possible to ship more than 700,000 volumes abroad in the past year. It is hoped to double this amount before the Book Center closes. The books and periodicals which your personal or institutional library can spare are urgently needed and will help in the reconstruction which must preface world understanding and peace.

Ship your contributions to the American Book Center, c/o The Library of Congress, Washington 25, D. C., freight prepaid, or write to the Center for further information.

# ZYGODACTYLY AND ASSOCIATED VARIATIONS IN A UTAH FAMILY

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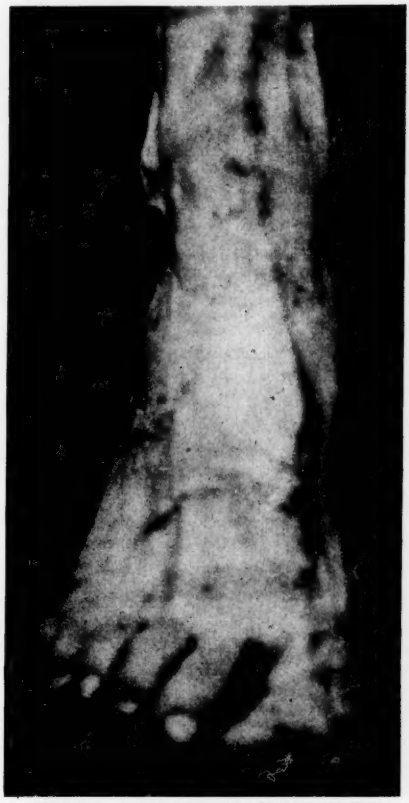
MOST of the pedigrees of syndactyly and zygodactyly† reported show a fairly constant phenotype within a given family. The following pedigree is submitted because of the irregularities of expression which it reveals. It is impossible to present entirely satisfactory statistical data on the mode, or modes, of inheritance because of our inability at present to say how many of the phenotypically normal persons are carriers of the mutant alleles.

Our observations concern two unrelated zygodactylous families, *A* and *B*, which have intermarried in one instance. It is possible that a different gene or genes may be involved in the two lines. The trait occurring in Family *A* is probably transmitted by multiple genes some of which may be sex linked. There are too few individuals in Family *B* to warrant definite conclusions.

Six generations including more than 350 "direct line" descendants of Family *A* have been studied. They include 21 phenotypically affected individuals and three persons shown by their descendants to be genotypically affected. All data concerning both Family *A* and Family *B* were gathered by the author, who has interviewed numerous members of both families. Information regarding those individuals not personally interviewed was obtained from other members of their families and after a lapse of one year all data were rechecked. See chart. (Figure 9.)



**ZYGO-, SYN- AND POLYDACTYLY**
**Figure 8**

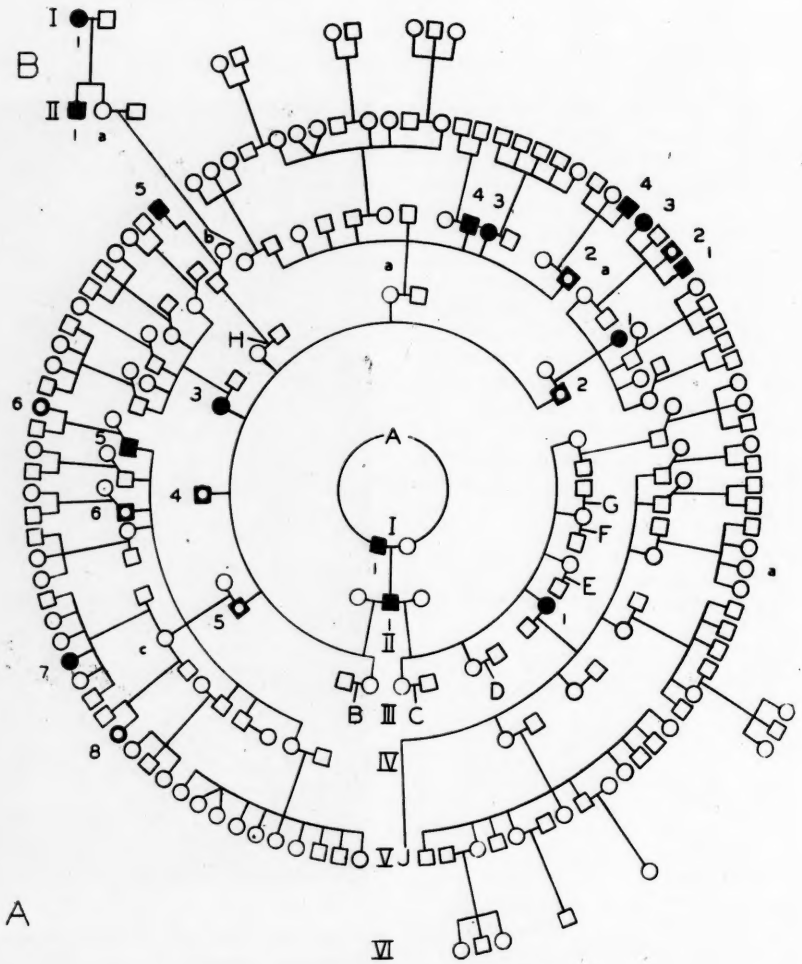
The right foot of III-2 is characteristic of the complex exhibited in the *A* Family. Zygodactyly is manifested in the connection between digits 4 and 5, and digit 5 is syndactylous with an incipient extra little toe. When zygodactyly expresses itself in the hand in this family, the webbing is usually between digits 3 and 4; when in the foot, between digits 4 and 5.

## Family A

The progenitors of Family *A* came to this country from Denmark in the late 1850's. Nothing is known about the

*The author wishes to express appreciation to Professor C. H. Danforth for his helpful suggestions in the presentation of this article.

†Zygodactyly is the term suggested by Weidenreich[6] for "webbed digits," morphologically distinguished from "syndactyly," which Schultz[4] prefers to limit to cases of skeletal fusions between phalanges in hands and feet.




**TWO ZYGODACTYLOUS FAMILIES**

**Figure 9**

Of the 23 affected individuals, 20 are in Family *A*, two in Family *B*, and one (V-5) is the child of a marriage between the two families. Solid black symbols indicate zygodactyly. Black with white centers mark individuals with extra phalanges. Other variations of the trait are given in detail in Table I. Individual V-7, for example, is also syndactylous. The *A* pedigree shows an interesting variety, not only in the range of its expression but also in the pattern of its transmission.

Generation III, lines B through H, and generation V, line J, have been left incomplete in the chart, since no descendants have shown the trait.

hands and feet of the parents of I-1, of his wife, nor of any of their children other than II-1. Of the more than one hundred individuals marrying into the family only one (IV-b from Family *B*) has ancestors known to be zygodactylous. Table I summarizes the expression of the trait in affected members of the *A* family.

## Family B

In Family *B* zygodactyly appears in its more usual form. Here the second and third digits of the foot are united, at least proximally (Table II). This type is illustrated in the figures presented by Stiles and Hawkins.[5] The condition is said to occur in about one person in a thousand in the general population. When the hands are also involved, the third and fourth digits are most often united. This apparent difference in the site of expression of the same gene in hand and foot is not surprising when it is recalled that normally the morphological axes are different, that of the hand passing through the third digit; that of the foot through the second.

## Discussion

Family *A* presents a less common deviation in which the third and fourth

**TABLE II.—Individuals in Family *B* affected with zygodactyly, and a description of the extent of development of the trait.**

| Individual | Member affected feet | Digits united | Comment |
|---|---|---|---|
| I-1 | both | 2-3 | Webbing between middle and proximal phalanges only. |
| II-1 | both | 2-3 | Same as I-1. |

**TABLE I.—Individuals in Family *A* affected with zygodactyly, and a description of the extent of development of the trait.**

| Individual | Member affected Hands | Feet | Digits United | Other Expression |
|---|---|---|---|---|
| I-1 | R | | 3-4 | |
| II-1 | R | | 3-4 | |
| III-1 | R | | 3-4 | |
| III-2 | | both | 4-5 | Extra appendage (middle and distal phalanges only) syndactylous with fibular side of 5th digit. |
| III-3 | both* | | 3-4 | |
| III-4 | | both | 4-5 | Identical with III-2. |
| III-5 | | both | 4-5 | Identical with III-2. |
| | R | | | Rudiments of extra digit syndactylous with middle and distal phalanges of little finger. |
| IV-1 | R | | 3-4 | |
| IV-2 | R | | 3-4 | |
| | L | | | Distal and middle phalanges of a "postminimal digit" fused to ulnar side of little finger. |
| IV-3 | both | | 3-4 | R zygodactylous and "double" nail on 4th digit, L* syndactylous. |
| IV-4 | R† | | 3-4 | |
| IV-5 | R | | 3-4 | |
| IV-6 | R | | | Similar to III-2. |
| V-1 | R | | 3-4 | |
| V-2 | both* | | 3-4 | |
| | | both‡ | | Additional digit on fibular side. |
| V-3 | R* | | 3-4 | |
| | L | | 3-4 | |
| V-4 | R* | | 3-4 | |
| V-5 | | both | 2-3 | "Webbing" between middle and proximal phalanges only. |
| V-6 | | R | | Extra appendage (middle and distal phalanges only) syndactylous with little toe. |
| V-7 | R | | 3-4 S | (Surgery not yet completed.) |
| | L† | | 3-4 S | |
| V-8 | R* | | 3-4 | Additional proximal phalanx on ulnar side of 4th digit. |
| V-a | | | | A foot deformity which is neither a clubfoot, polydactyl, syndactyl nor zygodactyl. Normal in all other respects. |

NOTE: S in the "Digits United" column indicates syndactyly. All other digits there listed are zygodactylous. Also, all surgical attempts are noted.

*Surgery failed to improve function.

†Surgery improved function.

‡Surgery successfully removed the polydactyl digits.

digits in the hands and the fourth and fifth digits in the feet tend to be united. This suggests either that the major gene is different in the two families, or that at least one important modifying gene present in the one is lacking in the other. If individual V-5 inherits his zydodactyly from Family *B*, it follows that the gene in Family *B* may be carried unexpressed for at least two generations.

The occurrence of extra phalanges which parallel the little finger and toe in certain individuals (Figure 8) of Family *A* should probably be interpreted as a kind of incipient polydactyly with concurrent zygodactyl connections between digits 4 and 5 and syndactyl connections between digits 5 and 6. (See Table I.) Whether these cases represent separate mutations or are themselves variants of the underlying genetic complex is uncertain, but distribution of the two traits in the descendants of III-a suggests the latter (Figure 9). This woman's digits are normal, although she has four zygodactyl sibs. Of the latter, three (III-2, III-4, III-5) are also syndactyl and polydactyl. Married to a normal husband III-a has eight children, one of whom (IV-4) is zygodactyl, another (IV-3) is both syndactyl and zygodactyl, and a third (IV-2) is polydactyl, syndactyl, and zygodactyl. IV-2, as shown in Table I, is not zygodactyl in the manner typical of this family. None of his three children are polydactyl, but one is typically zygodactyl. Similarly III-5, who is polydactyl, syndactyl and zygodactyl, transmits polydactyly through a non-polydactyl but zygodactyl son; and supernumerary phalanges, syndactyly and zygodactyly through a normal daughter. This suggests that the different manifestations are essentially interchangeable.

The individuals are all normal except as indicated. There is no record of intermarriage or illegitimacy; mentality is average or above, with only two cases of mental disorders, one being acquired (traumatic psychosis), the other congenital. In neither of these cases does the individual have abnormal digits. The family belongs to a sect which shuns the use of alcoholic and other "harmful" beverages, tobacco, etc. The above mentioned facts fail to support the suggestions of Edwards,[1] Knox,[2] and Murphy[3] that syndactyly is associated with such characteristics as low mentality, alcoholism and inbreeding.

### Comment

Some of the features in Family *A* that are of special interest are the following:

1. The appearance of the affected digits is not constant. Zygodactyly may appear in both hands or in the right hand only; it may occur in the feet but not in the hands. Thus far it has not occurred on a left appendage unless the right homologue was also affected.

2. There are three instances of "skipped" generations.

3. The six cases (III-3, IV-2, IV-3, V-2, V-3, V-7) in which digits of both hands were affected occurred in four females and two males. Two of the females (III-3, IV-3) have married and have twenty descendants, none phenotypically affected. These cases taken by themselves would have led one to suspect that the trait is sporadic rather than hereditary, but the pedigree as a whole shows that such cannot be the case. The affected male (IV-2) has three children, a male (V-4) being affected.

4. The five cases (III-2, III-4, III-5, V-2, V-5) in which digits of both feet were affected occurred only in males, and in contrast to the preceding, the two men who married (III-2, III-5) have 52 descendants of whom nine are phenotypically affected and two (IV-a, IV-c) are known to be genotypically affected.

5. The affected women have 69 descendants, none phenotypically affected. This suggests that affected females do not transmit the trait.

6. The "double" nail in case IV-3 is slightly wider than a normal nail while the length is approximately equal to that of the normal nail. One portion of the nail is wider than the other; the two

being separated by a small amount of integument. Cases III-2, III-4, III-5, V-2 have six normal nails on each foot (See Figure 8). These deviations indicate that there are numerous "modifying factors" apparently including sex influenced factors, altering the expression of this trait which is ordinarily assumed to be transmitted as a simple autosomal dominant.

### Inefficacy of Surgery

In only two cases (IV-4, V-7) has surgical separation of the "webbed" digits been successful in establishing normal use of the fingers. In six cases (III-3, IV-3, V-2, V-3, V-4, and V-8) the operation was unsuccessful in this respect. Various attempts have been made to explain the failure of many operations on "webbed" digits. Yatzoula[7] states that in a case which he studied the third and fourth digits of the left hand were joined only as to soft parts. Nerves and muscles were normal but the superficial volar arch had only two branches: a small one to the fifth digit and adjoining surface of the fused digit, a large branch in the third interosseous space and between the fused digits. The digital artery of the second interspace had a normal distribution but came from the deep volar arch. However, in the present pedigree there is no definite evidence that the vascular, muscular and nervous elements are abnormal. The explanation of surgical failure in these cases was tentatively given as due to the accumulation of scar tissue on the volar surface of the digits; nevertheless, removal of this tissue and grafting of new integument has not eliminated the contracture in the case of V-8.

### Conclusion

The ultimate cause of syndactyly and zygodactyly is undoubtedly one or more mutant genes, but the expression, as indicated in the present paper, and in others in this JOURNAL and elsewhere, is such as to suggest a great deal of plasticity in the developing digits and the probability that many different genes may affect development in similar, or even identical fashion. The subject is one which would justify a thorough comparative study.

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### Sonic Mousetrap Pictures by John Corcoran

The remarkable series of photographs of the convulsive departure from this world of dilute brown mice, illustrating Calvin Hall's article "Genetic Differences in Fatal Audiogenic Seizures," (JOURNAL OF HEREDITY, January 1947) were made available to us by Mr. John Corcoran of *Science Illustrated*. The photographs should have been credited to Mr. Corcoran and to *Science Illustrated*. We deeply regret that this was not done.—ED.

# HEVEA: A FIRST INTERPRETATION

## A Cytogenetic Survey of a Controversial Genus, with a Discussion of Its Implications to Taxonomy and to Rubber Production

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THIS is a first attempt on my part to interpret *Hevea* Aubl., genus of the Pará rubber tree. During a two-year investigation the genus was observed throughout much of the Amazon Valley. A cytogeographic analysis of *Hevea* was made by fixing material—usually leaves—and examining it "on the spot," or by bringing the fixed material back to a place convenient for study. Herbarium and wood specimens were collected. A representative living assemblage of plants was established at Belém, Pará, Brazil. Specimens in various herbaria have been examined; the literature has been rather well covered.

It would be tedious to give explanation here for the names which I use. Suffice it to say, first, that as a genus of great economic importance and yet poorly understood, *Hevea* has been subjected to an inordinate amount of "naming," and, second, that I consider the genus to consist of nine species† or fewer, if one chooses to make certain reductions which I will suggest. The accepted species are listed, but without regard to relationships:

*H. Spruceana* (Benth.) Muell. Arg.
*H. Benthamiana* Muell. Arg.
*H. viridis* Huber
*H. confusa* Hemsley
*H. rigidifolia* (Spruce ex. Benth.) Muell. Arg.
*H. pauciflora* (Spruce ex. Benth.) Muell. Arg.
*H. guianensis* Aubl.
*H. minor* Hemsley
*H. brasiliensis* (Willd.) Muell. Arg.

The list needs to be qualified somewhat. Until types are studied, one cannot be certain of the names to be applied to the entities here designated *H. confusa* and *H. rigidifolia.*

Chevalier[4] gives the reasons for the authority here used for *H. brasiliensis.* Until the type of *H. minor* is examined, one cannot be certain that the proper epithet is applied to this anomalous aggregate, which shows affinity to *H. Benthamiana* (with which it frequently hybridizes) and to *H. pauciflora* and is suggestive of extra-generic relationship, perhaps with *Cunuria* or *Micrandra.* *H. minor* was found on the Rio Uaupés as a bottle-butted tree, at the Venezuelan border as a treelet to ten feet, and along the Rio Negro in *estradas* with *H. Benthamiana* and of stature comparable to that of representatives of *H. Benthamiana.* A year-old seedling of *H. minor* was observed in flower. *H. viridis* should probably be reduced to synonymy under *H. nitida* Muell. Arg.

*The survey on which this study is based was made by the author as Agent (Associate Cytologist), Division of Rubber Plant Investigations, Bureau of Plant Industry, Soils and Agricultural Engineering, U. S. Department of Agriculture.

The interpretation is that of the author and is not necessarily in agreement with that of the United States Department of Agriculture. This paper is only slightly changed from the one read before the General Section of the Botanical Society of America at St. Louis, Missouri, in March, 1946, and which is abstracted in the *American Journal of Botany* for that month.

The author is greatly indebted to Dr. E. W. Brandes, who understood the importance of a cytogeographic survey of *Hevea,* and to Dr. Felisberto Camargo, who extended cordial cooperation and support during the period July, 1942, to July, 1944, while the study was being made throughout much of the Amazon Valley.

†Ducke[5] considered the genus to consist of twelve species, and Schultes,[14] of about twenty.

Introgressive hybridization has occurred to such an extent in *Hevea* that at some points specific lines lose their identities. This is not to say that recognizable entities do not exist in this genus. They do. But in nature and in various localities entities so intergrade that if one wished—and were not hesitant to be cumbersome in his treatment—he could, I think, reduce the genus to one species and consider it in terms of trinomials with many forms appended. Hybridization seemingly occurs whenever opportunity offers. As stated above, I prefer to recognize nine—or fewer—species and to formulate a genetic and cytological concept of their relations and to evaluate their ecological preferences.

Except for one clone of *H. guianensis* with a $2n$-number of 54 chromosomes and except for the possible occurrence of a race of *H. pauciflora* with 18 chromosomes, the genus apparently has throughout the greater part of its geographic range and for its various expressions a $2n$-number of 36. It is likely that this is a tetraploid condition. References to the several published counts of chromosomes for the genus are not stated here: that information will be brought together in another place.

Clone 5535 of *H. guianensis* at the Belterra Ford Rubber Plantation has a $2n$-number of 54. Meiosis is very irregular. Bivalents and univalents are usually present, though sometimes at diakinesis there are 27 bivalents. Metaphase I is always erratic with much precocious anaphase movement. At metaphase II groups of several chromosomes are frequent, but as many as 34 entities are found. Tetrads of four apparently normal microspores are rarely produced: two giant and two smaller microspores of varying sizes and one, two, three or four minute microspores are, as a rule, formed from a single pollen mother cell. As many as five nucleoli of diverse sizes are often present. These observations suggest that the plant is hexaploid (with six sets of nine) rather than triploid (with three sets of 18). This plant is referable to *H. guianensis* var. *marginata* Ducke and evidently came from the vicinity of Manáos, Amazonas. John Zilles (conversation) reports that the clone is difficult to bud. Fruiting is sporadic or not at all.

The material obtained on my Rio Negro trip to the Venezuelan border and up the Rio Uaupés was brought back to Manáos, Amazonas, for examination. From a fixation of *H. pauciflora* a preliminary count $2n$ of 18 was made, and the material discarded, for seed of that same collection had been got for planting at Belém: the seedlings were later found to have a $2n$-number of 36.

Though puzzling, the aberrant count is significant: perhaps a race of *H. pauciflora* with 18 somatic chromosomes exists. The species is seemingly an old one: it occurs on the hills that rise abruptly out of the flat country of the upper Rio Negro region. Those hills are old: they stretch in discontinuous fashion down from ancient formations in Venezuela. This *seringa* (*seringueira*) *da serra* will doubtless be found on the geologically old formations in Venezuela and the Guianas. The tree is suggestive in its general aspect and in seed characters of *H. brasiliensis*. It seems likewise to form a transition to *H. Spruceana*. Also, the look of its foliage reminds one of *H. minor*. As I observed it, the species is without value for its latex, but according to Spruce (Bentham[3]) it yields a "very copious milky juice." Specimens collected on the Orinoco by Aimé Bonpland and early confused with *H. brasiliensis* are possibly correctly referred to *H. pauciflora* (see Chevalier[4]). Perhaps via Trinidad or by way of botanical gardens in the Guianas, *H. pauciflora* has entered the plantations of the East and has been masquerading as *H. brasiliensis*. Thus the report by Heusser[7] of a $2n$-number of 16, $n$-number of 8, for *H. brasiliensis* may be accounted for as an approximation of a diploid condition. Both for scientific and for practical reasons it is very important that the various hills mentioned above be explored in the expectation that races of *H. pauciflora* will be found: in the

whole analysis of *Hevea* no problem is more urgent. This species is probably the prototype of *H. brasiliensis* and was likely one of the parents of *H. rigidifolia*.

Consideration of the species from the standpoint of their ecological preferences is of great help in understanding the genus. The Amazonian natives have in many instances given the plants ecological names and have not been too unsuccessful in differentiating the species: in fact along the Rio Negro, the natives have, in my opinion, done a better job than some of the botanists in recognizing the entities.

Often the ecological situations for *Hevea* are contiguous, and then hybridization frequently occurs, especially if the vegetation has been disturbed, as by man. Most of the hybrids probably do not survive, but survival is more likely when new ecological situations have been created. Under natural conditions selection tends to fix ecotypes and to eliminate variants away from that tendency. Because of that, and since an infinitesimally small percentage of ovules fertilized in nature produce mature plants, seeds and seedlings taken from the wild afford a more accurate and varied sample of the genetic make-up of a population than do mature individuals in nature or propagates from them. However, hybrids involving various species were found in nature by the writer: they are preserved as herbarium material. In nature hybrids often occupy situations different from those of the parents, so that introgression with a third species may take place.

About all that any individual in a balanced tropical forest does is to replace itself. It is not likely that the proportion of the constituent species in such a complex association changes very much with the passage of time, unless the environment is modified. In the case of *Hevea* one is apt to find young trees where the fall of a forest giant has opened a considerable space to light. This seems important, though the Amazonian forest is, as a rule, rather open and with mature plants of many different heights within a given area. Except in the openings, young trees of *Hevea* are not often encountered: the vast majority of the seedlings die within a few weeks.

In the vicinity of towns and cities in the Amazon Valley new situations are continually being brought into existence by the cutting down of the surrounding forests for fuel, and, to a lesser extent, for agricultural purposes. Add to this the inclination of the native to spare *Hevea* as a producer of latex, or, in some areas, because the seed are eaten, or because the wood is poor fuel, and one readily sees that excellent opportunities are there for hybrid swarms to become established. Moreover, trees of *Hevea* in the open flower sporadically and thereby afford increased chance of overlapping of flowering periods. Then consider that botanists have collected most intensively in the neighborhood of villages, and one of the reasons is clear for the reputation of *Hevea* as a taxonomically difficult genus.

Illustrations of hybridity in the vicinity of towns may be cited.

Some years ago Ducke described *H. gracilis* from the outskirts of Manáos, Amazonas, and later—properly, I think, —diagnosed the plant as a hybrid of *H. guianensis* × *H. Benthamiana*. From that same area—in fact from trees fifty feet away from *H. gracilis*, Ducke described *H. Huberiana*, which he later gave varietal status under *H. Benthamiana*. From the same population he also described a form of this species, and from that area var. *marginata* of *H. guianensis*. In recognition of the usual habitats of these species the natives often refer to *H. guianensis* as *seringa da terra firme*—rubber tree of unflooded or high land, and to *H. Benthamiana* as *seringa da igapó*—rubber tree of flooded areas. It is my opinion that destruction of precise ecological differences between these habitats made it possible for a hybrid population to become established.

In the marshes around Iquitos, Peru, is what I consider to be a hybrid swarm of *H. confusa* × *H. guianensis*. The former is a purplish-fruited, small tree

of the *catingas* of the upper Solimoes region, along the upper Rio Negro and in the Guianas, Venezuela, Colombia, and Peru. Possibly, also—as via *H. camporum*—in eastern Amazonas. The *catinga* has a very characteristic vegetation, of which *seringa da catinga* is usually an element. From that population at Iquitos, Ule described *H. paludosa,* and Ducke named *H. humilior.* The plants are doubtless extracts from a hybrid swarm, with strong resemblance to *H. confusa.* A similar population is at São Paulo de Olivença, Amazonas.

At São Gabriel on the Rio Negro one finds intergrades of the distinct *seringa da serra* (*H. pauciflora*) which is characteristic of the hills of that region and of *H. confusa.* Possibly on the basis of that very population Ducke has made these two species varieties of *H. pauciflora.*

In the open country at Benjamin Constant on the Rio Solimoes, Ducke found a tree which he considered to be intermediate between *H. guianensis* and *H. lutea,* and for this and comparable reasons he and Schultes have recently made *lutea* a variety of *H. guianensis* (Schultes[12]). One might with almost as much reason render the genus unispecific.

*H. Spruceana* is known from the confluence of the Rio Iça with the Solimoes and down to the islands at the mouth of the Amazon and, throughout this region, along the lower reaches of the tributaries of the great river. The species is found along the sluggish waters of those streams and is especially characteristic of the low places which lead off from the streams and which become flooded during the rainy season. The trees may or may not have their roots in water the year round. They are small trees with little latex and that of poor quality. The flowers are bigger than those of any other species and are nearly unique in their purplish color: a collection of *H pauciflora* exhibited this color character. The fruit (suggestive of that of *Cunuria Spruceana*) and seed are the largest in the genus, and the carpels remain on the tree after the fruit explodes. The trunk is greatly swollen at the base; this causes the appropriate name, *seringa barriguda* —big-bellied rubber tree. But *H. minor* and *H. Benthamiana* may have a similar enlarged stem.

Along the northern tributaries of the Amazon and some of the tributaries of the Solimoes, *H. Benthamiana* occurs in many localities adjacent to *H. Spruceana,* and farther up those northern rivers, as the Rio Negro for example, and in Venezuela, Colombia, and perhaps Peru, it frequently occupies the places where one would expect to find *H. Spruceana* if it were in the region. *H. Benthamiana* is about the same size as *H. Spruceana,* or considerably larger, has smaller fruit and seed, does not retain the carpels after the seed fall, has small and yellow flowers, has reddish rather than white pubescence on the lower leaf surface, and produces good latex. It is perhaps second to *H. brasiliensis* in the quality of its latex: density of population often compensates for the small size of the trees. It usually has a swollen trunk.

In 1943 at the first rapids on the Rio Trombetas I found hybrids of *H. Spruceana* and *H. Benthamiana:* downstream there seemed to be only *H. Spruceana;* upstream, presumably, only *H. Benthamiana.* In the spring of 1944 at the Belterra Rubber Plantation I examined a population of several hundred trees that had been established as *H. Benthamiana* and brought as seedlings from the lower Rio Negro. The trees were flowering and fruiting for the first time. Represented were *H. Spruceana* and *H. Benthamiana* and segregants from interspecific crossing. About the hybrids there could be no doubt: as indicated above the species have many contrasting characters. Ducke[6] described such a hybrid. Occurrence of these two entities in adjoining areas along the edges of streams and bodies of water facilitates their hybridizing and causes a situation somewhat different from that to be expected of species dispersed in forests. Since these plants hybridize with such readiness they may perhaps eventually

be relegated to a single species with proper subspecific or varietal recognition, and in spite of marked morphological differences. If so, then what is to be done about *H. brasiliensis?*

In places *H. brasiliensis* grows adjacent to *H. Spruceana* and, as Ducke[5,6] has, I think, correctly reported, crosses with it. I found such a plant on the Rio Juruá. And it is my feeling that *H. brasiliensis* of the islands at the mouth of the Amazon has been infiltrated with genes from *H. Spruceana:* the stature of some of the trees suggests that, and the rubber from those islands is well known for a peculiar adhesive and weak quality, which, I believe, has a certain advantage for special commercial uses. Moreover, though *H. Spruceana* reaches those islands and the habitats are favorable, occurrence of the species there seems restricted. It is of interest that Huber[9] thought that some of the *brasiliensis* seed from the islands suggested hybridity with *H. Spruceana*—and others seemed to show influence of *H. guianensis;* he accordingly proposed selection by size of seed that were to be planted—in the expectation that seed of hybrids and of other species than of pure *H. brasiliensis* would be eliminated. Indeed a recent publication has indicated the possible value of biometric studies in selecting seed of *H. brasiliensis* in Malaya. It is considered in the East that mixed plantings of *brasiliensis* and *Spruceana* hybridize readily.

Parenthetically, I might mention that Schmöle[16,17] reported with regard to certain AVROS clones that rootstocks of *H. brasiliensis* × *H. Spruceana* have proved experimentally to be superior to *brasiliensis* rootstocks: growth was better on the former as evidenced in the "development of crown and stem, in a greater thickness of untapped and renewed bark, and in greater number of latex vessels," and yield was "notably better." Schmöle's "hybrid" seed were from open-pollinated trees of *H. Spruceana* intermixed with *H. brasiliensis:* the seed resembled those of the former species; the growth habit of the seedlings resembled that of the second. One should be able to determine in seedling stages whether or not the plants from *Spruceana*-like seed were hybrids.

According to Ducke,[6] the Amazonian natives recognize the hybrid origin of individuals that result from the natural crossing of these two species in the designation *seringa casada*—married rubber tree. It is the opinion of that author that fifteen such hybrids studied by him in the vicinity of Manáos, Amazonas, exhibit less variation, except for seed characters, than would a similar number of representatives of either parental species. I found the chromosome number of two of those hybrids to be the same as for the parental species—$2n=36$, and meiosis to be regular.

Sorensen[18] has indicated that ten acres of a 50-50 mixture of *H. Spruceana* and *H. brasiliensis* will be planted in Colombia for production of hybrid seed to furnish rootstocks. That demonstrates great—and, in my opinion, unjustified—confidence in the small-scale experiment of Schmöle. In no statement that I have read about hybrid rootstocks has any mention been made of genetic variability in the parental species. Yet, anyone who has examined *Hevea* knows that so great is the variability that very little study of each individual tree of the genus is necessary to separate it from the others, on morphological characters alone. For characters of complicated heredity—such as superior rootstock quality, it can not be predicted prior to experiment what the results of hybridizing particular individuals will be.

Just as I would consider the infiltration of *Spruceana* into *brasiliensis* of the islands, I would similarly weigh the possibility of introgression of *H. viridis* into *H. brasiliensis* to produce var. *subconcolor* of the latter species. This variety occurs in the region of the upper Solimoes and in Peru and Colombia, and where the two species are in contact. Other reports extend this range. Sterile type material from the Solimoes is close to that of *H. viridis,* which is present there. In January, 1943, I collected the variety

at the type locality and established buddings at Belém. There the typical variety (as well as *H. viridis* from Borba on the Rio Madeira) exhibits remarkable resistance to *Dothidella ulei:* the fungus makes mere minute lesions on the leaves and causes no real injury. And Sorensen[18] records that in plantings in Colombia *H. brasiliensis* var. *subconcolor* (he does not give the varietal name) is so resistant to South American leaf blight that "it can grow right beside severely diseased material of Eastern derivation without being affected at all." As the variety has spread, the typical character has to a degree been lost, probably through genetic selection toward *H. brasiliensis*. R. J. Seibert (conversation) questions the validity of the variety.

There would likewise appear to be genic influence of *H. brasiliensis* on *H. viridis*. In establishing the latter species Huber[8] mentioned that it was a tree of about sixty feet in height that grew in the same places that *H. brasiliensis* does. It is altogether possible that the species is typified by the variety of *H. brasiliensis* mentioned above. Huber used sterile material, and, unfortunately, a tree transplanted by him from the type region in Peru to the Museu Goeldi in Belém has only recently flowered, but I have not seen specimens. As I know the species on the Rio Madeira and in the upper Rio Negro region, it is a tree of about thirty feet and restricted to the *catingas,* where one would not expect to find *H. brasiliensis*. In Colombia Schultes[13] has found *H. viridis* as a "very robust tree" in *igapós* and as a "medium sized and poorly developed tree" on rocky hillsides and sterile places near falls; he likewise published the bushy or shrubby var. *toxicodendroides* Schultes and Vinton, from certain sandstone mountain-tops in Colombia. It is pertinent to this whole discussion that seed collected by me in February, 1943, from a single tree of *H. viridis* in the *catinga* forest near Borba on the Rio Madeira and planted at Belterra and at Belém segregated into low- and high-branching treelets. I last saw those plants in July, 1944, so I can not say whether or not they have developed into shrubs and trees. Under forest conditions the shrubs—if they are actually such—would have little chance of survival; in open places, as *campo* or mountain-top, they would. A tree of *H. viridis* at the mouth of the Uaupés was unusual in having hard heartwood.

In a recent report on *H. rigidifolia*[2] I considered this species* and *H. confusa, H. pauciflora,* and *H. viridis* to be expressions of the same complex. They have hybridized many times in nature. And it is my opinion that *H. camporum,* a treelet described by Ducke from a *campo* east of the Rio Madeira, will be found to have the same relation to *H. confusa* that var. *toxicodendroides* does to *H. viridis,* they perhaps being ecotypes and nothing more.† In fact, *H. confusa* and *H. viridis* may eventually be combined.

By the same reasoning that has been applied above, one might find explanation for the excellent rubber of the Acre Territory of Brazil and of the neighboring regions in Bolivia and Peru. Populations of *brasiliensis* there, by virtue of geographic remoteness from *H. Spruceana*—and from certain other species of little latex-value, as *H. viridis*—would be expected to be relatively free of gene contamination with respect to quality and quantity of latex. But, in addition, another biological factor would

*On March 18, 1944, I found a small population of *H. rigidifolia* beside a streamlet that meandered from the top of a low hill on the south side of the Rio Uaupés and about midway between Taracuá and Bella Vista: Montepelago, Amazonas, Brazil. The trees—some of them estimated to be seventy feet high—were with mature fruit. Cytological and herbarium material were taken from two trees (*Baldwin 3669, 3670*), and seedlings were established at Belém. It appears that these are the first or second collections since Spruce's.

†This interpretation of relationships was presented orally to R. E. Schultes in January, 1945. That author (1946[15]) affirms, with a statement from A. Ducke, this concept.

seem to have had a chance to operate for the superiority of the trees of those areas: representatives of *H. brasiliensis* are huge in that region and rise to or above the ceiling of the forest; pollination may possibly, therefore, take place over vast distances, and trees of different geographic areas and of different populations may in time, perhaps through intermediate individuals, be crossed. And this would seem to be particularly likely if pollination is by winged insects, as stated by Rands[10]: they might go in bee line from one tree to another. And what is the significance of this?

Perhaps no two sexually produced individuals are alike; they may differ in genes or in gene arrangement or in chromosome number. And for each genetic change that occurs others are requisite. As a sexual species propagates itself, populations unique in their genetic make-ups become established in the various parts of the specific range. Members of the same population are apt to have a more similar genetic mean than members of different populations. Environmental selection, internal or external isolation, and the spread of variability by chance or otherwise, depending on population size, all help to cause this. Therefore, for example, if yield in *H. brasiliensis* is controlled by one thousand genes,* an individual taken at random in a population might have the recessive alleles of a hundred of those genes; an individual from another population might also be recessive for a hundred genes, but many of them would be different from the hundred of the first individual. And similarly with respect to individuals from each population of the species. Furthermore, if maximum yield is dependent on all the thousand genes being present in a dominant state, it would appear that the best—in fact, the only, directed way of approximating the optimum would be by routine hybridization (whether natural or artificial) of random individuals from different populations. It would seem that conditions for this to occur are satisfied for *H. brasiliensis* in Acre Territory and adjoining areas. By this means too a gene, or group of genes, might conceivably flow throughout the range of the genus.

In various parts of its range, and especially in Matto Grosso—where, interestingly enough, *H. guianensis* is apparently represented by none of its varieties—*H. brasiliensis* has yellow-latexed individuals in addition to those with latex of the usual white color. It is considered here that genes for that condition have entered the species from var. *lutea* of *H. guianensis* and that the character has spread over wide areas even though the parent species is not known or is infrequent in those areas. Naturally, mutation could be the basis for this condition. The suggestion is made here that *H. brasiliensis* may have evolved out of hybridization of *H. pauciflora* with *H. guianensis* var. *lutea*. Some trees of this variety produce latex of excellent quality.

Now for a practical consideration of the theoretical concept that has been developed. As is well known, South American leaf blight is the limiting factor, other than soil and labor, to the establishment of extensive *Hevea* plantings in this hemisphere. An effort has been made to avoid the disease by grafting resistant tops on clones that have proved to have high yields. Attempts have also been made to cross high-yielding Oriental clones with resistant trees. (The Eastern material is highly susceptible to leaf blight.) Finally, native trees that the workers have demonstrated to be high-yielders have been selected and propagated in the hope that they would maintain under conditions of cultivation their yield and also be highly resistant to *Dothidella*. None of these approaches appears to me to be practicable for a

*Yield, being the end-expression of the whole physiology of the plant, is controlled by the interaction of hundreds of genes, and changes in the chemistry of any one of many of those genes, or the introduction of one or a few key alleles into the gene association, might markedly curtail production.

long-time plantation program. Of course, top-working is a means of salvaging plantings that have already been made and has great value as an emergency measure. But surely, since resistance to *Dothidella* is of complex heredity, one would be reluctant to use the highly susceptible material from the East in every cross. Moreover, since one can tell almost nothing about resistance under forest conditions, it is hazardous to select individual trees from the jungle solely on the basis of production, and, for that matter, yield might not be maintained under other conditions. Accordingly, suggested here are three approaches to the disease-yield problem which is basic to plantations for the Americas.

The most practicable approach seems to be to establish huge seedbeds at several places in Acre and adjoining regions where the quality and quantity of latex of *brasiliensis* is renowned; to inoculate the seedlings in the seedbed with *Dothidella* of different geographic sources (for the fungus consists of different strains), and to establish testplots of the most resistant seedlings, selected insofar as possible to show no character of another species. This procedure was suggested in December, 1943, without favorable reception.

Second, it would seem important to collect seed and seedlings from places in nature where species overlap and where hybrid individuals are found and to grow thousands of those individuals to maturity at field spacing. Thus segregates of all degrees could be grown, and the labor and time incidental to artificial hybridization could be avoided.

Third, a long-time breeding program should be inaugurated whereby individuals of *H. brasiliensis* from various geographic sources would be crossed in random fashion, and hybrid individuals grown to maturity at field spacing. For, if the statements made above with reference to yield are true, they hold equally well for other characters of complex inheritance, as, for example, disease resistance.

Breeding for yield in *Hevea*—and in most other plants—has usually been by self-pollination or by hybridization of plants of promising productivity followed by selection through comparative yield tests. Such concentration on high-yielding plants is not necessarily the best procedure in a long-time breeding program; indeed it most likely is not. Selection for yield is almost surely accompanied by the "selection out" of some of the factors critical to the optimum expression of the desired character. However, for *Hevea* and for most tropical plants, so little has been done that almost any approach gives positive results.

For experimental material the various kinds of *Hevea* need attention, and plants of certain areas should be especially considered. The Uaupés area of Brazil is the center of generic variability.[1] Intensive study of the region is most desirable. Seven of the nine species that I accept are there, including the anomalous *H. minor* and the apparently endemic *H. rigidifolia*. Three species of *Cunuria* are there: this genus is close to *Hevea* and exhibits certain parallel variations. And *Micrandra*, of close affinities to *Hevea* and *Cunuria*, is also well-represented. On a clear March afternoon one may stand at a single spot and hear the varied tempo of fruit-explosions and seed-falls of species of all these genera. And one sees various individuals of *Hevea* of doubtful specific reference; some of them by their huge size and few fruits suggest that they are wide hybrids. And as one travels by boat along the lower Uaupés and for long distances above and below its confluence with the Rio Negro the varying degrees of intensity of green in the leaves of *H. guianensis* var. *lutea* are striking; it is as though the species were segregating with genes from *H. viridis*, which is common there. If one cuts the thick outer covering of the capsules of some of those trees of var. *lutea*, the purplish pigment so characteristic of the fruits of *H. viridis* and *H. confusa* will be seen.

The varied series of habitats associated with the aged hills rising sharp-

**AMAZON TRIBUTARIES**

**Figure 10**

Outline sketch map of South America, showing the rivers which are mentioned in the accompanying discussion of *Hevea*. The Uaupés area is the center of variability for this genus.

ly out of the Amazonian plain in that region suggests a reason for the complexity of the genus and of its allies there: ecological selection has had great amplitude within which to work, and possibly likewise with segregates from wide hybridization. And *H. pauciflora —seringa da serra*—atop some of those hills seems to be the oldest representative of the genus that one knows. A buttressed tree of the species causes one to speculate on possible affinity with *Cunuria.* It is of interest in this connection that the natives of the upper Rio Negro region eat the seed of *C. Spruceana* and of *H. pauciflora,* and that, though they designate the latter tree *seringa,* they say it has seed like *cunurý.* Perhaps, then, it is, in part, one of the derived species of *Hevea.* Introduced into cultivation the fast-growing seedlings of *H. pauciflora* promise to be of practical value for rootstocks.

Geological evidence indicates that the Amazon Basin has been subject to a number of cataclysmic changes. Seemingly, it once had an outlet to the west, conceivably along the Rio Negro-Rio Uaupés route. Elevation of the Andes changed the direction of flow—maybe first southeastward to the Atlantic along the present Guaporé-Paraguay-Paraná system, and later by the Amazonian debouchment.

Reversals in water-flow, rise and subsidence of land-masses—these critically influence the distribution and evolution of organisms. Alone, these happenings produce one sort of organic picture; with the added effect of glaciation,—as, for example, in North America, quite a different one. When a species spreads it usually becomes differentiated geographically into populations, each with a characteristic genetic equilibrium. Populations are disjunct, or, sometimes, peripherally contiguous. Tilting—one might almost say "sloshing" with regard to the Amazon Basin—disturbs individuality of populations and the established areas of species. Most importantly, new ecological situations are brought into being, and old ones are disrupted. Accordingly, representatives of different genotypes come wthin breeding range: hybridizations—especially in regions historically free from temperature shocks, where the incidence of polyploidy might be assumed to be low—and segregations occur: two ecotypes hybridize and transition to a third one is made.* This "tilt" theory affords one explanation for the extreme richness of the Amazonian flora, a richness characterized more perhaps by populations and ecotypes and aberrant individuals than by distinct species.

Such diversity for *Hevea,* as mentioned above, is expressed in the upper Rio Negro region, particularly in the Uaupés area. That may well prove to be one of the most meaningful floristic areas in South America. On a hurried trip there I observed extreme variability for *Hevea, Cunuria,* and *Diospyros.* Correlations and causes should be sought in the geology of the region.

Precise knowledge of the phytogeography of South America will give many insights into the geologic history of that continent. And surely an accurate mapping of the different kinds of *Hevea*—one of the genera most typical of the Amazonian flora—and of its allies, especially *Cunuria, Micrandra,* and *Joannesia,* will contribute greatly to an understanding of the story of the Amazon Valley.

If one assumes for the Amazonian region a one-time inland sea, he might envision *Cunuria* along the slight heights of its shores. The genus is not uncommon in the upper Rio Negro-Orinoco-Uaupés region. As *C. Spruceana—cunurý da terra firme*—it has been collected in eastern Colombia and in Brazil at São Paulo de Olivença on the Rio Solimoes and off the Rio Madeira in the

*This idea was brought into sharp focus by an oral statement of R. J. Seibert that in some individuals of *Hevea* the characters of three species can be recognized: I am in agreement with that statement.

Municipality of Humaytá. The genus is known, questionably by two species, from the upper Mazaruni drainage in British Guiana. Designation of hills off the Rio Trombetas in Brazil as "cunury mountains" is evidence that the genus is there. Are these records not suggestive of a likely outline for our hypothetical lake? If so, then the geographic occurrence of the *pauciflora-rigidifolia-confusa-viridis* aggregate of *Hevea* takes on added meaning. This is an old complex of the genus which covered a vast area. It is well represented in the Guianas and in the upper Rio Negro-Orinoco-Uaupés region and is known at Iquitos in Peru, and in Brazil at São Paulo de Olivença on the Rio Solimoes and at Borba on the Rio Madeira and, via the so-called *H. camporum,* from the headwaters of the Rio Marmellos, an eastern tributary of the Madeira. It occupied the hilltops and was on many of the formations with *Cunuria* and was especially frequent just back from the shoreline of that hypothetical inland sea.

Geologic happenings disrupted the ecologic continua to which the *confusa-viridis* plants were adapted: the preferred situations are now present as *catingas. H. guianensis,* widespread also, became diverse through many hybridizations and developed many ecotypes. Was *H. Spruceana* on the very shores of that sea and, with it, did it recede to the sluggish waters near the Amazon; and, receding, did it leave genes dispersed in some of the plants of the upper Rio Negro region? Did not that species evolve perhaps through intermingling of the genotypes of *Hevea* and *Cunuria?* And perhaps *H. rigidifolia* and *H. minor* also? And should not one begin to suspect the genotype of *H. Benthamiana* since it hybridizes in such a ready and widespread manner with the cunurioid *H. Spruceana* and *H. minor?* And one is tempted to try to develop *Micrandra* out of *Hevea* and *Cunuria.* And *Joannesia?* At least it can be said that it appears to be diploid and not tetraploid as those other genera seem for the most part to be. However, not enough is known of the genera of this phase of the Euphorbiaceae to allow too great a freedom for speculation.

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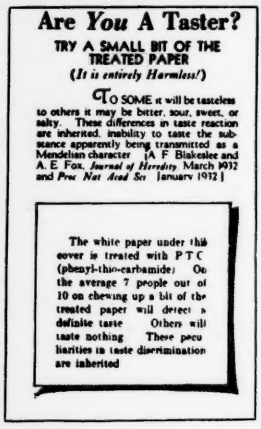
## Genetics Congress Date

Word has just been received in the United States that the Eighth International Genetics Congress will be held in Stockholm, July 7-14, 1948. Additional announcements regarding pre-congress demonstrations are promised soon.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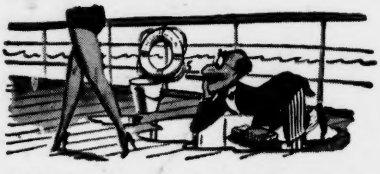

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